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The control of saccadic adaptation: implications for the scanning of natural visual scenes

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Abstract

Accurate scanning of natural scenes depends on: (1) attentional selection of the target; (2) spatial pooling over the attended target to compute the precise landing position; and (3) adaptive modification of saccades to ensure saccadic accuracy. The present experiments studied adaptation. Adaptive modifications were induced by displacing the target during saccades. Adaptation was found to be: (1) similar for a small target point and a large target circle, despite the differences in the spatial pattern of landing position errors for each; (2) unaffected by instructions to look part way to the target, even though such instructions altered landing position error relative to the target; and (3) insensitive to symbolic cues disclosing the direction of the intra-saccadic displacement. Briefly delaying the presentation of the post-saccadic target greatly reduced adaptation. Neither corrective saccades, nor the position errors that trigger corrections, were involved in adaptation because corrective saccades rarely occurred with a large target circle even though the circle produced as much adaptation as the single point. Taken together, the results do not support the traditional notion that post-saccadic retinal position error controls adaptation. We propose that adaptation relies on a comparison of the actual post-saccadic retinal image with the post-saccadic image that would be predicted based on a representation of the planned saccade. Such a comparison: (1) is consistent with our results; (2) may be more effective than retinal position error in controlling adaptation in natural visual scenes containing large targets and backgrounds; and (3) is similar to the motion-based adaptive mechanisms associated with the VOR. Similarity between the adaptive control of saccades and adaptive control of the VOR raises the possibility that the most important role of saccadic adaptation may be the coordination of eye and head movements during shifts of gaze.

Keywords: Saccadic eye movements; Attention; Adaptation; Eye–head coordination; Efferent copy

1. Introduction

Saccadic eye movements are crucial for the performance of visual tasks. They bring selected objects to the fovea, providing a sequence of high-resolution views of the most informative sections of the scene. The importance of obtaining detailed visual information means that the performance of visual tasks will be limited by the effectiveness of saccadic control.

Two characteristics of natural scenes pose challenges to achieving effective saccadic control. First, the selected targets are usually surrounded by extraneous visual backgrounds. For saccades to be accurate, the influence of the backgrounds must be reduced or eliminated, and the saccadic programs based on the targets alone. Second, the selected targets are typically spatially-extended objects or regions, not specific locations within them. Some process is needed to operate on the visual information in the selected object or region and determine precisely where the saccade will land.

Below is a brief summary of the attentional and visual processes that allow saccades to cope with these two challenges, visual backgrounds and spatially-extended targets. Then, we will introduce and describe new experiments on saccadic adaptation. Saccadic adaptation is the process by which saccadic parameters are modified on the basis of past performance to ensure accurate eye movements in the future. The summary that follows of the way in which saccades cope with backgrounds and large targets is relevant to the adapta-

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tion experiments because the experiments will also focus on finding out how the error signals that initiate adaptation are compatible with the constraints imposed by the backgrounds and large targets in natural scenes.

1.1. Selective attention controls the choice of the target in the presence of backgrounds

Selective perceptual attention designates the target of a saccade, determining which visual signals are 'seen' and processed by the saccadic system, and which should be ignored. Studies using dual-task methods (concurrent measurements of saccadic and perceptual performance) have verified the links between saccades and perceptual attention by showing that saccadic performance suffers (longer latencies; poorer accuracy) when attention is withdrawn from the saccadic target and allocated elsewhere (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher & Blaser, 1995; Deubel & Schneider, 1996). The attentional requirements of saccades are real but modest: considerable attention can be paid to locations other than the saccadic goal with no performance loss (Kowler et al., 1995). The link between saccades and perceptual attention means that looking at a target requires no separate attentional filtering, beyond what would be a natural part of the performance of the task, namely, taking an interest in some area remote from the line of sight when the task requires it, and initiating a saccade as soon as detailed information is needed.

1.2. Spatial pooling determines the landing position of the saccade within large, attended targets

The natural targets for saccades are objects — faces or words, for example — yet each saccade must land at only one location. The specific location need not be deliberately selected. Instead, when saccades are aimed toward an attended object, the line of sight lands effortlessly, and with a high level of precision, near the target center (He & Kowler, 1991; Guez, Marchal, Le Gargasson, Grall & O'Regan, 1994; Kowler & Blaser, 1995). Precise landing positions have been found for patterns of random dots (McGowan, Kowler, Sharma & Chubb, 1998), as well as for various simple shapes (Melcher & Kowler, 1999). The high level of precision of saccades directed to large targets implies that landing position is determined by pooling across the attended shape. (For discussions of pooling in a different situation, namely, small targets surrounded by distracters, see Findlay, 1982; Ottes, Van Gisbergen & Eggermont, 1985; Coëffé & O'Regan, 1987; He & Kowler, 1989.)

1.3. Saccadic adaptation ensures saccadic accuracy

In addition to the selection and pooling processes described above, saccadic accuracy also depends on adaptive control. Saccadic adaptation can be demonstrated in the laboratory by displacing the target while a saccade is in progress, a technique introduced by McLaughlin (1967). Initially, saccades are in error, but within a few trials saccadic amplitude adjusts, bringing the line of sight close to the final location of the target. This sort of rapid adaptation is sometimes viewed as the laboratory version of the slower adaptive modifications that are found to occur in natural situations as a result of oculomotor muscle paresis (Scudder, Batourina & Tunder, 1998).

Studies have shown that the rate of adaptation increases when fewer target locations are tested (Miller, Anstis & Templeton, 1981; Albano & King, 1989; Scudder et al., 1998) and that adaptation trained at one location transfers, at least partially, to nearby locations (Miller et al., 1981; Wolf, Deubel & Hauske, 1984; Frens & van Opstal, 1994; Chaturvedi & van Gisbergen, 1997). Recent human neurophysiological studies have indicated that the cerebellum is a major control site of adaptation (Desmurget, Pelisson, Urquizar, Prablanc, Alexander & Grafton, 1998), a conclusion that agrees with that drawn from earlier studies of patients with eye muscle paralysis (Optican, 1985) and neurophysiological studies of adaptation in monkey (Goldberg, Musil, Fitzgibbon, Smith & Olson, 1993; Frens & van Opstal, 1997).

The rapid rate of adaptive changes suggests that the saccadic system is continually and automatically adjusting the links between visual location and motor commands. Despite its importance for maintaining accurate saccades, significant questions remain about the conditions, both visual and behavioral, that initiate and control adaptive modifications of saccades.

1.4. The initiation and control of saccadic adaptation

Adaptive changes in saccadic amplitude could be triggered by the detection of the retinal position error that is present whenever saccades miss the target, where retinal position error refers to the retinal eccentricity of the target after the saccade lands (McLaughlin, 1967; Miller et al., 1981; Wallman & Fuchs, 1998). No one has asserted that retinal position error is the only, or even the most important, error signal controlling saccadic adaptation because it has several obvious shortcomings. Specifically, retinal position error is well-defined when the target is a single point, but is harder to define under more natural conditions, with visual scenes containing large targets surrounded by backgrounds. A valid assessment of retinal position error in the presence of backgrounds requires a process-

ing stage that distinguishes error with respect to the selected saccadic goal from error with respect to the other visual objects in the scene. Also, when the targets for saccades are objects of some spatial extent, it is not obvious how to define retinal error. It can be defined with respect to a reference location within the target or with respect to local regions along the contour.

Some have proposed that other, perhaps less problematical, error signals could initiate, or at least contribute to, saccadic adaptation. For example, efferent signals accompanying the secondary, corrective saccades might play a role (Albano & King, 1989). Wallman and Fuchs (1998), however, showed that corrective saccades are not exclusively responsible for adaptation. Others have suggested that adaptive modifications might depend on a visual process that compares the post-saccadic position of all or parts of the retinal image with the positions that would be predicted based on the size and direction of the planned saccade (Deubel, 1991; Bahcall & Kowler, 1999). Mismatches between actual and predicted retinal images would trigger adaptive modifications whenever systematic or random errors at some stage in the generation of the saccadic command prevented the saccade from being executed as originally planned. Cognitive factors could also be involved in adaptation. Investigators have discounted the possibility that adaptation results from a deliberate strategy of adjusting saccade size in anticipation of the imposed intra-saccadic displacements because subjects usually do not notice the displacement (Wolf et al., 1984; Goodale, Pelisson & Prablanc, 1986; Erkelens & Hulleman, 1993). However, cognitive factors can play more subtle roles in oculomotor control. For example, anticipatory smooth eye movements are not planned deliberately (Kowler & Steinman, 1979), but are, nevertheless, sensitive to symbolic cues disclosing the direction of future target motion (Kowler, 1989). It is possible that saccadic adaptation, like anticipatory smooth eye movements, also depend on high-level cognitive cues.

The present paper investigated saccadic adaptation under conditions that varied both the nature of the available visual error signals and various cognitive components of the task. In the initial experiments, adaptation to intra-saccadic displacements of a single point target was compared to adaptation to displacements of a large target (outline drawing of a circle). These two types of targets were tested to find out whether adaptation would be comparable despite the differences in the spatial configuration of the position error signals available after the saccade lands (see the discussion above of point vs. large targets). The comparison of point vs. large targets also provides a way of evaluating the role, if any, of corrections, since corrective saccades are very rare with large targets (Kowler & Blaser, 1995). A follow-up experiment examined the role of visual error signals by delaying the appearance of the post-saccadic target, a manipulation that did not change the spatial parameters of the visual error signal.

Experiments also examined the effect of higher-level factors. This was done by: (1) asking subjects to look only 75% of the way to the target (thereby creating retinal error with respect to the visual target, but not with respect to the chosen saccadic goal); and (2) providing a symbolic shape cue that was correlated with the direction of the intra-saccadic displacement.

We found that saccadic adaptation was not disrupted either by using large targets or by deliberately aiming saccades only part way to the target. Adaptation was also insensitive to symbolic visual cues disclosing the direction of the intra-saccadic displacement. The only condition that seriously disrupted adaptation was a delay in the appearance of the post-saccadic target. Accounting for these results would require several modifications of the traditional retinal error model. A promising alternative, however, is for adaptation to be controlled by a comparison of the post-saccadic retinal image with the image that would be predicted based on the size and direction of the planned saccade. Such a signal, unlike retinal position error, should be as effective in natural scenes, with their large targets and textured backgrounds, as in a dark laboratory with only a single point of light in the field of view.

2. Methods

This paper describes the results of five experiments. The subjects, eye movement recording and data analysis subsections below were common to all experiments. The stimulus conditions and procedure subsections below apply to the first, basic experiment (single-point target). Changes made in the subsequent experiments will be described later in the paper, along with the results.

2.1. Subjects

Two naive subjects (BS and EAB) and one of the authors (EK) were tested. BS and EK ran in each experiment, while EAB was tested in a subset. All had prior experience as eye movement subjects.

2.2. Eye movement recording

Two-dimensional movements of the right eye were recorded by a Generation IV SRI Double Purkinje Image Tracker (Crane & Steele, 1978). The subject's left eye was covered and the head was stabilized on a dental biteboard.

The voltage output of the Tracker was fed on-line through a low pass 50 Hz filter to a 12-bit analog to

digital converter (ADC). The ADC, controlled by an IBM compatible PC, sampled eye position every 5 ms. The digitized voltages were stored for later analysis.

Tracker noise level was measured with an artificial eye after the tracker had been adjusted so as to have the same first and fourth image reflections as the average subject's eye. Filtering and sampling rate were the same as those used in the experiment. Noise level, expressed as a standard deviation of position samples, was 0.4′ for horizontal and 0.7′ for vertical position.

Recordings were made with the tracker's automatically movable optical stage (auto-stage) and focus-servo disabled. These procedures are necessary with Generation IV Trackers because motion of either the auto-stage or the focus-servo introduces large, artifactual deviations of Tracker output. The focus-servo was used, as needed, only during intertrial intervals to maintain subject alignment. This can be done without introducing artifacts into the recordings or changing the eye position/voltage analog calibration. The auto-stage was permanently disabled because its operation, even during intertrial intervals, changed the eye position/voltage analog calibration.

2.3. Display apparatus

The target for the saccade was a single point generated by digital-to-analog converters and shown on a display monitor (Tektronix 608, P4 phosphor) located directly in front of the subject's right eye. The display was refreshed every 10 ms, a rate that was high enough to prevent visible flicker. The luminance of the display, measured by a UDT photometer (model 61) from a 2.2×2.2 cm region containing 1600 points refreshed every 10 ms, was 34 cd/m^2. The room was totally dark except for the target point itself. The stimulus was viewed through a collimating lens which placed it at optical infinity.

2.4. Stimulus conditions

Three types of stimulus conditions were tested: forward hop, backward hop, and no-hop. Each session began with 20 no-hop baseline trials in which the target remained stationary during the saccade. The baseline trials were followed by forward, backward, or no-hop adaptation trials (150 for EK and 110 for EAB and BS). In the adaptation trials the point hopped when the saccade was detected (see Section 2.5). The adaptation trials were followed by 50 no-hop trials for EK and 40 for EAB and BS.

2.5. Procedure

Before each trial subjects fixated a single point that was located 108′, 120′ or 132′ to the left of straight ahead (when rightward saccades were tested) or to the right of straight ahead (when leftward saccades were tested). The initial fixation point was offset from straight ahead to restrict eye movement recording to the central 5° of the visual field where tracker output is linear. Leftward and rightward saccades were tested in separate experimental sessions, as were forward, backward, and no-hop stimuli. After fixating the initial point subjects initiated a trial by means of a button press. 200 ms later the point was erased and redisplayed in a new location, either 228′, 240′ or 252′ away. Both the position of the fixation target (108′, 120′ or 132′) and the size of the target step (228′, 240′ or 252′) were selected randomly on each trial.

Subjects were instructed to make a single accurate saccade to the target. In order to discourage a strategy of deliberately increasing or decreasing saccade size in anticipation of the hop, subjects were reminded to aim the saccade to the target as seen before the saccade and not to be concerned with any post-saccadic errors they might notice. This same instruction has been used successfully in the past to encourage best possible accuracy of the first saccade and discourage a strategy of relying on secondary saccades to correct error (Kowler & Blaser, 1995; McGowan et al., 1998).

Eye position was monitored on-line and, following the detection of the saccade, the target was either hopped forward by 48′, backward by 48′, or not at all at the next refresh of the display. The point remained visible at the post-hop location for the remainder of the 2-s trial. The criterion for on-line saccade detection was a position change of more than 12′–15′ in 5 ms (40–50 deg/s). The small differences in criteria are due to differences in individual subjects' eye position/voltage output calibrations. In the no-hop sessions, and in the baseline trials at the beginning and end of sessions, the target point remained stationary during the saccade. After each trial the point reappeared at the start location for the next trial.

A replication consisted of six sessions: forward, backward, and no-hop for leftward and rightward saccades. The order of the hop conditions within a replication was selected randomly while saccadic direction (left or right) was alternated from session to session.

2.6. Analysis of saccades

The beginning and end positions of saccades were detected by means of a computer algorithm employing an acceleration criterion. Specifically, eye velocity was calculated for two overlapping 20-ms intervals. The onset time of the second interval was 10 ms later than the onset time of the first. The criterion for detecting the beginning of a saccade was a velocity difference between the samples of 300′/s or more. The criterion for saccade termination was more stringent in that two

consecutive velocity differences had to be less than 300′/s. This more stringent criterion was used to ensure that the overshoot at the end of the saccade would be bypassed. The value of the criterion (300′/s) was determined empirically by examining a large sample of analog records of eye position. Saccades as small as the microsaccades that may be observed during maintained fixation (Steinman, Haddad, Skavenski & Wyman, 1973) could be reliably detected by the algorithm.

The size of each saccade was defined as the distance between the mean position of the eye at the start of the trial (average of first 50 ms) and the position of the eye at the end of the saccade. By using eye position at the start of the trial, rather than eye position at the onset of the detected saccade, our estimate of saccade size also incorporated any drift (Kowler & Steinman, 1979) that might occur during the latency interval.

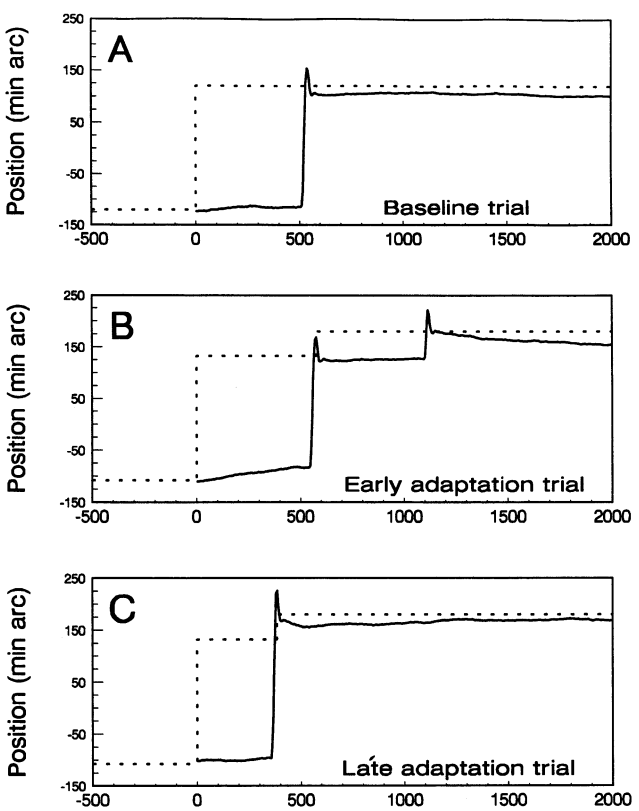

Fig. 1. Representative traces of horizontal eye (solid line) and stimulus position (dashed line). Negative position values are left of center. (A) Saccade in response to a 240′ target step. Saccade size is the difference between pre- and post-saccadic eye position, bypassing the overshoot at the end of the saccade (see Section 2). (B) An early adaptation trial, 48′ forward hop. (C) A later adaptation trial.

3. Results

3.1. Single point target

Fig. 1 shows an example of: (a) a baseline (no-hop) trial, (b) a trial containing a forward hop, taken from early in the experimental session, before adaptive effects were apparent, and (c) a trial taken from late in the session containing a forward hop, showing how adaptation reduced the error of the saccade.

The time course of adaptation to forward and backward hops of a single point target is shown in Fig. 2. The figure shows average saccade size in bins of 20 trials. Adaptive changes in saccade size were apparent within 20 trials and typically reached maximum levels within about 60-80 trials. By contrast, saccade size in the no-hop controls remained relatively stable, showing that the systematic changes in saccades observed during sessions with hops were not due to fatigue or to other extraneous factors.

The magnitude of adaptation was summarized by taking the difference between average saccade size in the final 50 adaptation trials in sessions with and without hops. During these final trials saccades in the forward hop sessions (averaged over subject and saccadic direction) were 24′ larger (50% of hop size) than saccades in the no-hop sessions. Decreases in saccade size in response to the backward hops was larger, with average differences between backward and no-hop session equal to 37′ (77% of hop size). The magnitude of adaptation, separated by subject, replication and saccadic direction, is summarized in Fig. 10 ('point').

Fig. 2 also shows the decay of adaptation during the final 40–50 no-hop trials (the portion of each plotted line located to the right of the vertical line in each graph). Saccade size began to return to baseline (pre-adaptation) levels within about 20 trials. Saccades did not always return completely, as indicated by the small, but consistent, differences between forward and backward hop sessions that remained in the final blocks of the session.

3.2. Circle target

Natural targets for saccades are objects, not points. This experiment tested adaptation with a target that was an outline drawing of a circle (diameter 3°), composed of 12 equally-spaced dots. As in prior experiments using spatially-extended targets, subjects were instructed to make a single saccade from the initial fixation point to the target circle as a whole and not to aim for any particular place within it (Kowler & Blaser, 1995; McGowan et al., 1998; Melcher & Kowler, 1999). Such instructions produce landing positions nearly as

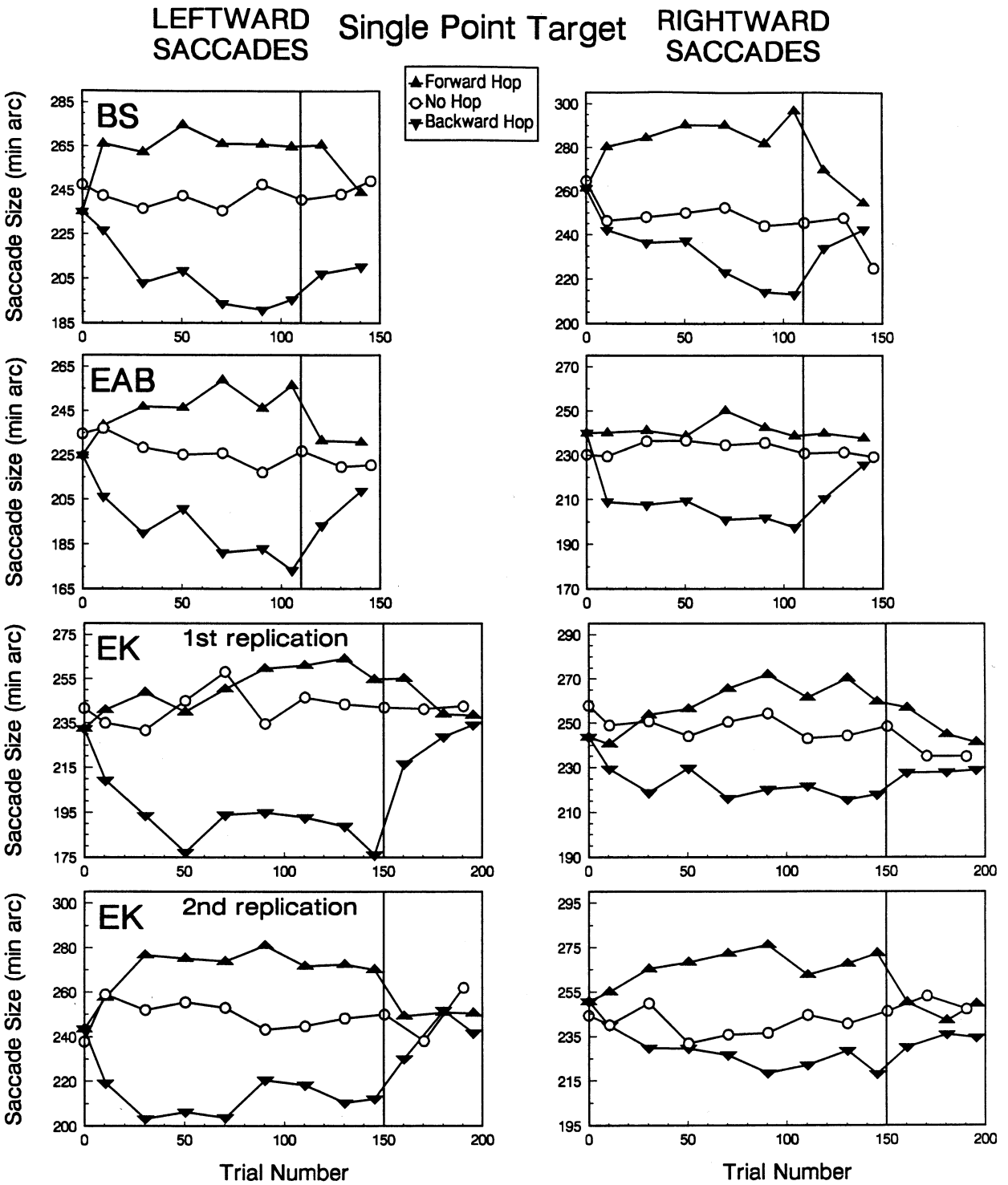

Fig. 2. Mean saccade size plotted as a function of trial number for the forward, backward, and no-hop conditions. Each symbol shows saccade size averaged over 20 consecutive trials. Results for three subjects, and two saccadic directions, are shown in separate graphs. The vertical line at trial 110 (BS and EAB) and trial 150 (EK) indicate when the adaptation trials ended and testing began with the post-adaptation no-hop trials. The symbol at trial 0 shows saccade size averaged over the 20 no-hop trials which preceded each session.

precise as those observed with single point targets.

Fig. 3 compares adaptation with the circle target to adaptation with the point target (point data are reproduced from Fig. 2). A second replication with the circle produced very similar results. Both the time course and magnitude of adaptation were quite similar for the different kinds of targets (see summaries in Fig. 10). Thus, using a target without a specifically marked landing position did not diminish the adaptive changes to saccades.

3.3. Corrective saccades: target points versus circles

Subjects were asked to avoid making secondary, corrective saccades in order to encourage best possible accuracy of the initial saccade (see Section 2). Under such instructions, secondary saccades become less frequent, particularly for large targets where corrections become extremely rare (Kowler and Blaser, 1995).

Secondary saccades were rare with the large target circle in the present experiment, as expected. Figs. 4 and 5 show trial-by-trial plots of the size and direction of secondary saccades made with both the point and circle targets. A secondary saccade was defined as any saccade that began within 500 ms after the initial saccade ended. This interval was used to isolate saccades likely to be involved in correcting errors of the first saccade, rather than look away from the target (Steinman et al., 1973).

Overall, 31–72% of the trials with point targets contained secondary saccades (depending on subject and saccadic direction). Of these 90% were corrective in the sense that they were in the direction of the intra-saccadic hop and, thus, typically reduced the error left by the initial saccade. By contrast, less than 20% of the trials with the circle targets contained secondary saccades, and of these 80% were corrective. Fig. 6 shows that the proportion of trials containing secondary saccades that were also corrective was much greater for the point than for the large circle target.

The critical finding is that the magnitude of adaptation was quite similar for point and circle targets (Fig. 3) despite the fact that a sizeable number of corrective saccades were found only with the point. This shows that corrective saccades are not responsible for saccadic adaptation.

3.4. Looking a fraction of the distance to the target

This experiment investigated the consequences of producing retinal offsets deliberately. Subjects were asked to aim the saccade only 75% of the way to the target. We wanted to know two things. First, would the deliberate shortfalls initiate adaptive changes similar to the adaptive changes produced by the intra-saccadic target hops? Second, would intra-saccadic hops continue to produce saccadic adaptation, even though, in this experiment, there was a large discrepancy between the size of the retinal offset with respect to the visual

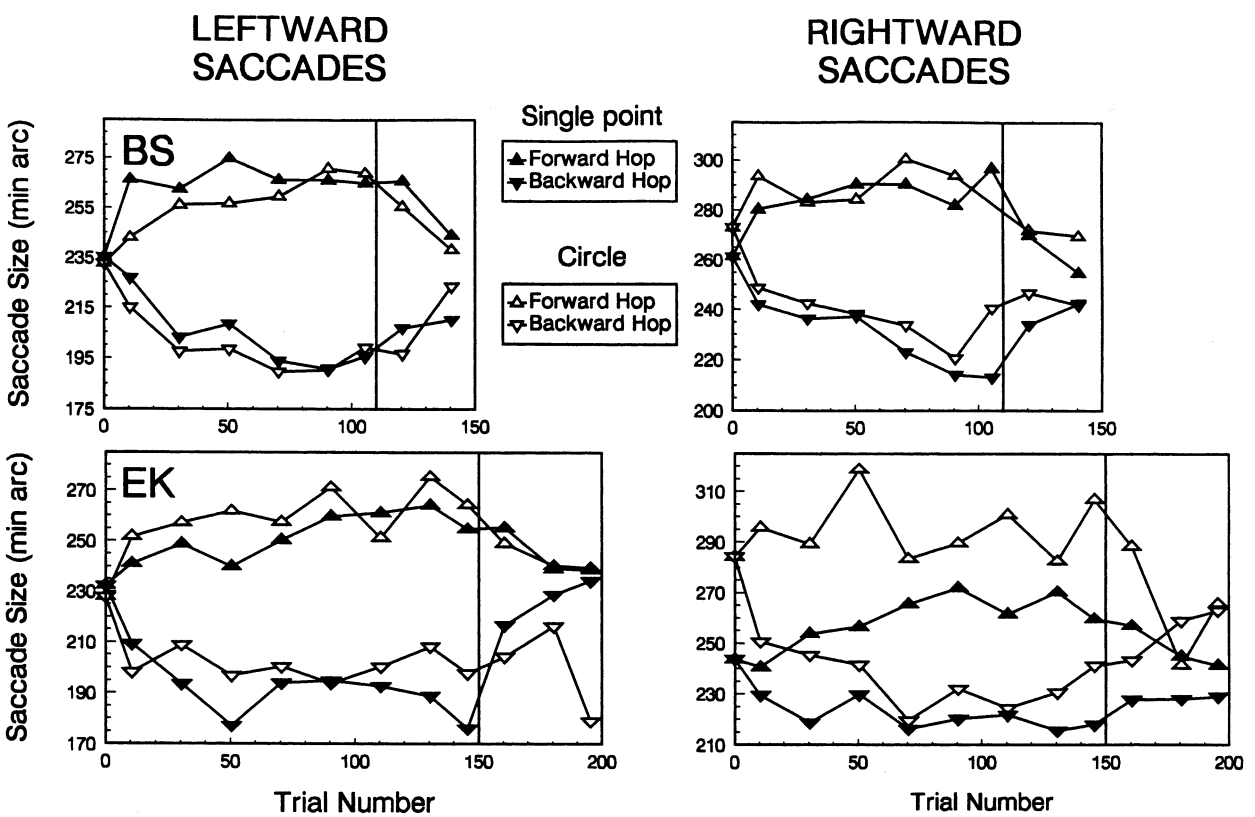

Fig. 3. Mean saccade size as a function of trial number for two subjects in the circle target experiment (open symbols) compared with data from the single point experiment (reproduced from Fig. 2). Each symbol shows saccade size averaged over 20 consecutive trials. Data are shown for two subjects, two saccadic directions and the forward and backward hop conditions. The vertical line at trial 110 (BS and EAB) and trial 150 (EK) indicate when the adaptation trials ended and testing began with the post-adaptation no-hop trials. The symbol at trial 0 shows saccade size averaged over the 20 no-hop trials which preceded each session.

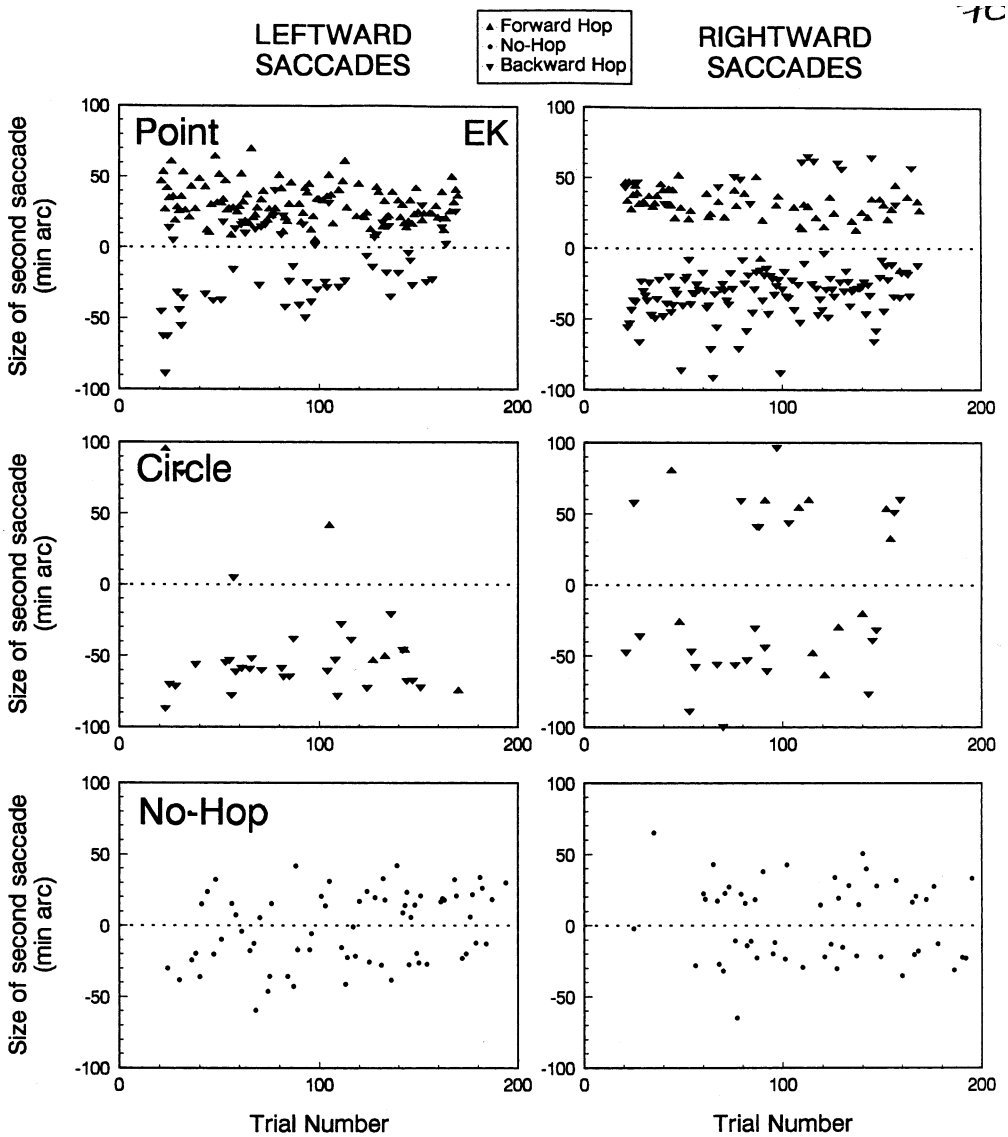

Fig. 4. Size of the second saccade on each trial as a function of trial number for subject EK when the target was a point or circle. Data from sessions without hops (point target) are also shown. For the point and circle conditions, saccade size is shown with separate plotting symbols denoting the forward and backward hop conditions. Positive values indicate secondary saccades in the same direction as the first saccade.

target and the size of the retinal offset with respect to the intended landing position?

The experimental conditions were the same as those in the first experiment (single point target) except that subjects were asked to look 75% of the way to the target. (For other examples of saccades under instructions to look somewhere other than directly at the target, see Steinman et al., 1973; Hallett, 1978.)

The time course of adaptive changes (two replications/subject) are shown in Fig. 7. (The second replication comes from sessions in which trials measuring perceived direction were interspersed; Bahcall & Kowler, 1999.) During the no-hop sessions saccades went about 75% of the distance to the target, in accordance with the instruction. Sometimes size decreased by up to 20′ (8% of eccentricity) throughout the session. If the error signal driving adaptation was retinal offset defined with respect to the visual target, saccade size should have increased through the session in response to the deliberate shortfall. At the very least, subjects might have been poor at maintaining the self-induced offset. The data, however, do not support this prediction. Saccades size either remained stable or decreased.

Saccades adapted during the sessions containing hops (Figs. 7 and 10), although the pattern of adaptation was more complex than in the basic experiment, where saccades were aimed directly at the target. BS's rightward saccades showed adaptive effects that were superimposed on a tendency for saccade size to decrease over time. Her leftward saccades were more stable and the typical pattern of adaptation can be seen. EK adapted to only the forward hops during the first replication. In

her second replication saccade size was more variable, and adaptive effects can be seen in all cases except the forward hops for rightward saccades.

Despite the variability of performance obtained under instructions to look 75% of the way, the occurrence of adaptation in the presence of hops, and the lack of adaptive correction of retinal offset in the no-hop condition, show that adaptation does not depend on the size of the retinal position error between the landing position of the saccade and the visual target. Changing retinal error with respect to the visual target by asking the subjects to land off target does not either promote or prevent adaptation. Thus, either the system controlling adaptation evaluates retinal position error with respect to the intended landing position of the saccade or, alternatively, the system is using a different sort of cue.

3.5. Delayed feedback

In all the experiments described thus far the target hop occurred during the saccade. In this experiment we examined what would happen if the feedback about saccadic accuracy were delayed. This was accomplished by briefly delaying the presentation of the post-saccadic point. The experiment was the same as the basic single point condition except that the target was erased during the saccade and the display kept blank for 400 ms before the point was displayed at the new, post-hop, location. This temporal delay meant that there was no visual feedback as to the accuracy of the saccade during the time period immediately following the saccade. If the error signal that drives adaptation is computed within this narrow time window, then adaptation should be disrupted by the delay.

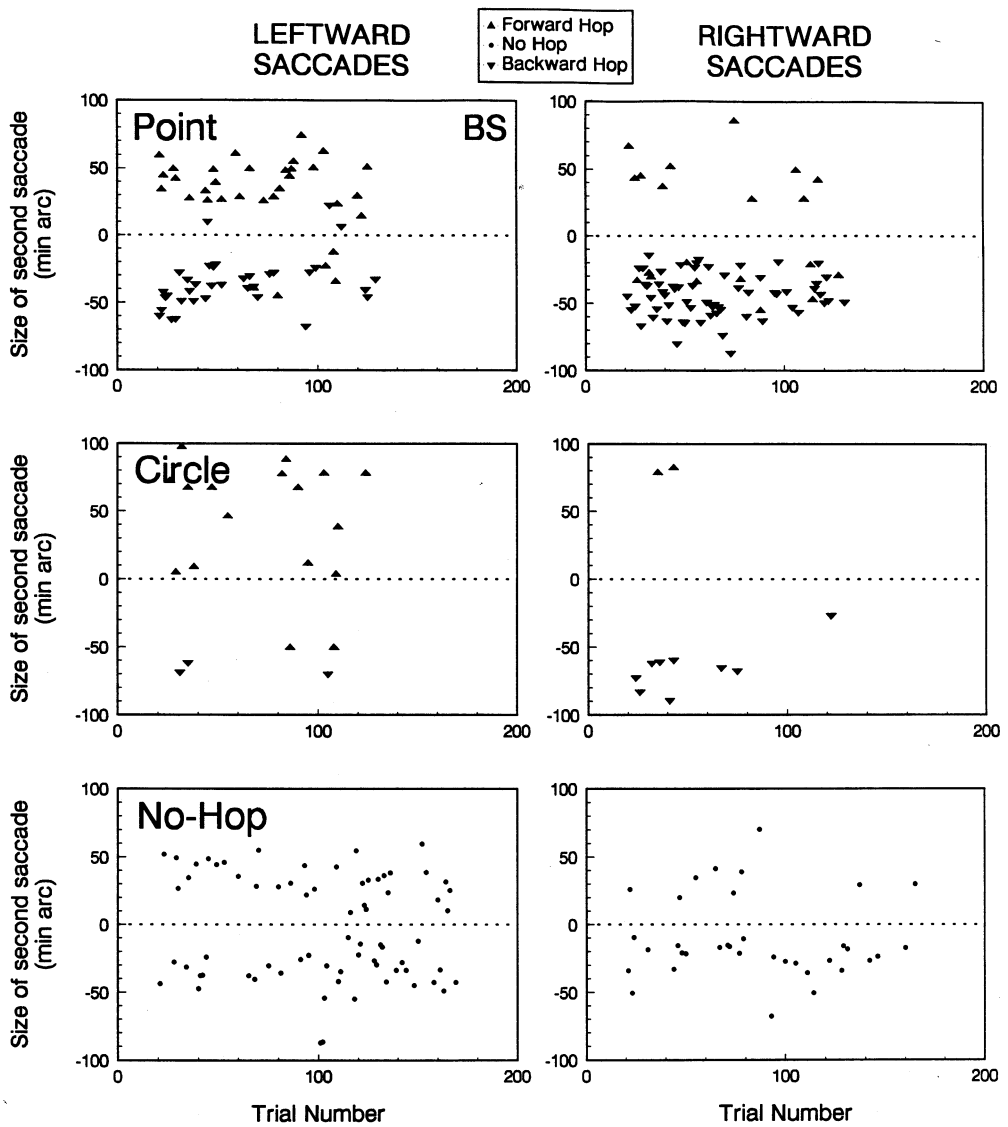

Fig. 5. Size of the second saccade on each trial as a function of trial number for subject BS when the target was a point or circle. Data from sessions without hops (point target) are also shown. For the point and circle conditions, saccade size is shown with separate plotting symbols denoting the forward and backward hop conditions. Positive values indicate secondary saccades in the same direction as the first saccade.

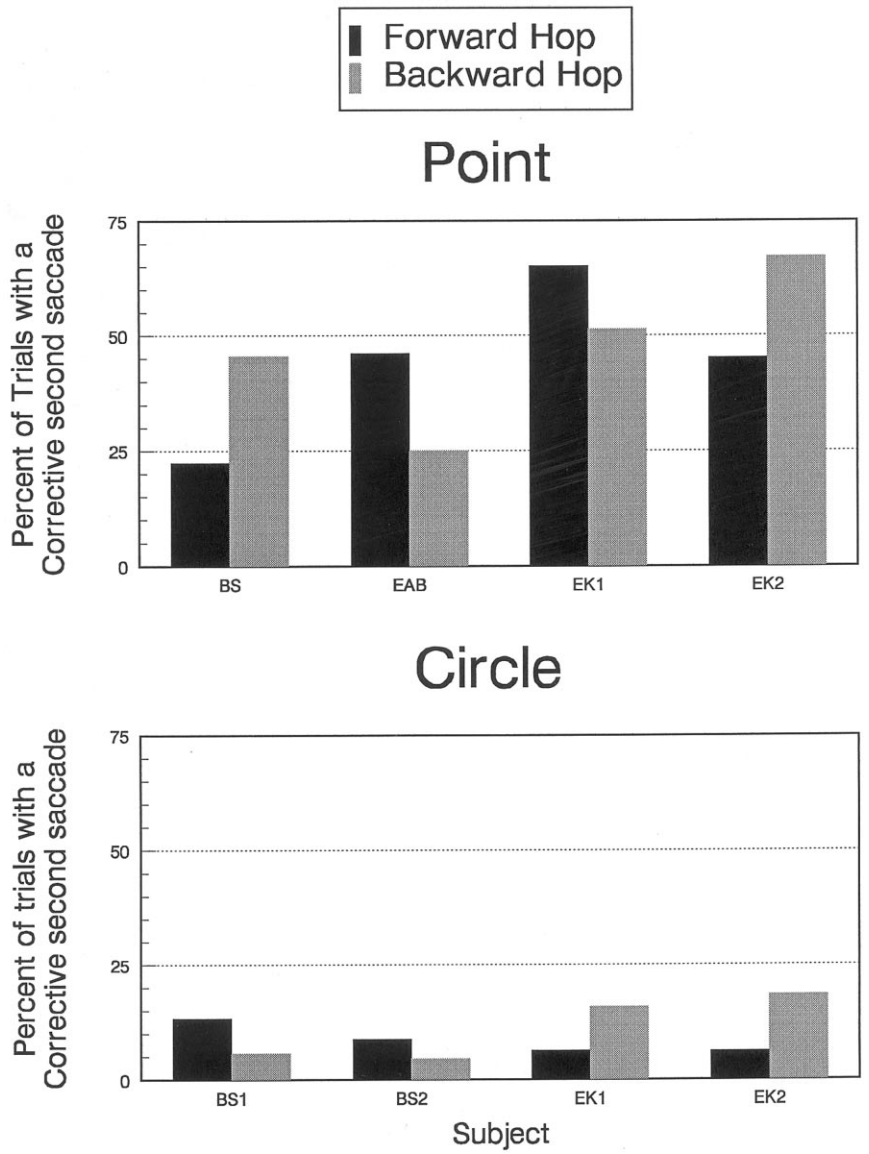

Fig. 6. Percentage of trials containing secondary saccades that were corrective (in the direction of the target hop). Data are shown for the forward and backward hop conditions in the point experiment (for subjects BS, EAB and EK, two replications) and circle experiment (for subjects BS and EK, two replications).

The results from the three subjects (BS, EAB and EK) are shown in Figs. 8 and 10. (These data were collected in sessions in which psychophysical trials measuring perceived direction were interspersed; Bahcall & Kowler, 1999.) The delay eliminated adaptation for BS and EAB and greatly reduced adaptation for EK.

The reduction of adaptation is interesting because the stimulus conditions were identical to those used in the basic experiment (single point target, Fig. 2) except for the 400 ms delayed appearance of the post-saccadic target. One interpretation of this result is that the error signal driving adaptation is computed immediately after the saccade is completed. Delaying the appearance of the post-saccadic target would interfere with such a computation.

The failure to produce adaptation when feedback is delayed is also relevant to the issue of the role of deliberate strategies in producing adaptive modification of saccades. As noted in the introduction, researchers generally dismiss the role of strategies because subjects usually do not notice the occurrence of the hops. The lack of adaptation in the present experiment strengthens the case against deliberates strategies. Why would a subject stop using a deliberate strategy of compensating for error just because a delay is introduced? If anything, such delays have been shown to improve the detectability of the hops (Deubel, Schneider & Bridgeman, 1996), and thus, one might expect delays to facilitate the use of such strategies.

3.6. Shape cues

This experiment examined whether a high level property of the stimulus, namely, shape, could influence adaptation. This issue was studied by attempting to adaptively increase the size of saccades made to one shape while simultaneously decreasing the size of saccades made to another. Prior work by Deubel (1995) addressed this issue by interspersing two stimulus shapes within an experimental session. One of the stim-

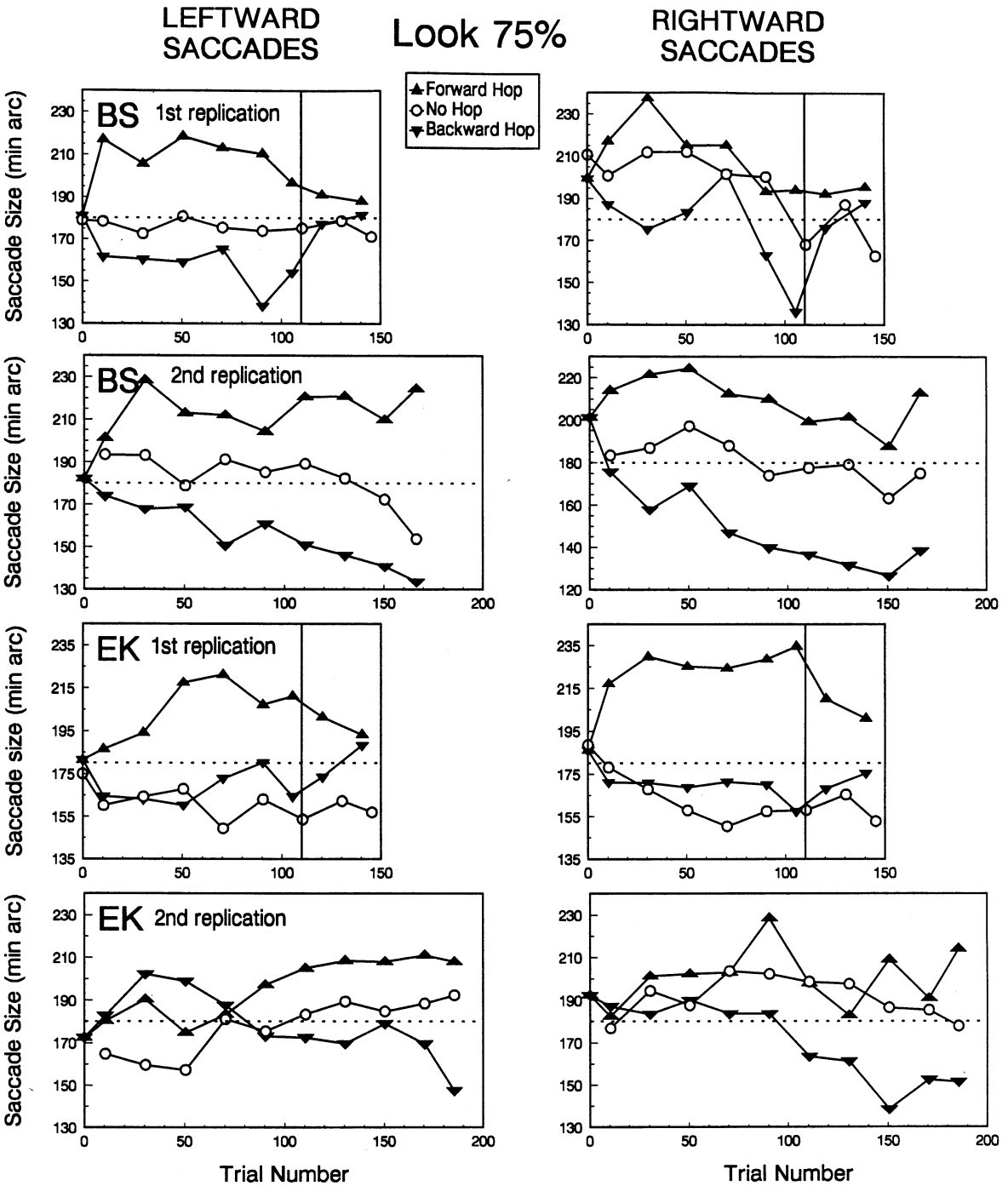

Fig. 7. Mean saccade size as a function of trial number under the instruction to look 75% of the distance to a single point target. Data are shown for two replications for two subjects, two saccadic directions and three hop conditions (forward, backward, and no-hop). Each symbol shows saccade size averaged over 20 consecutive trials. The actual location of the target would be shown at 240 min arc. The dashed line at 180 min arc indicates 75% of the distance to the target. The solid vertical line in the first replication for each subject indicates when the adaptation trials ended and testing began with no-hop trials. The second replication for subject BS and EK were run with perceptual localization trials (not shown) periodically interspersed after trial 90 (Bahcall & Kowler, 1999). The symbol at trial 0 shows saccade size averaged over the 20 no-hop trials which preceded each session.

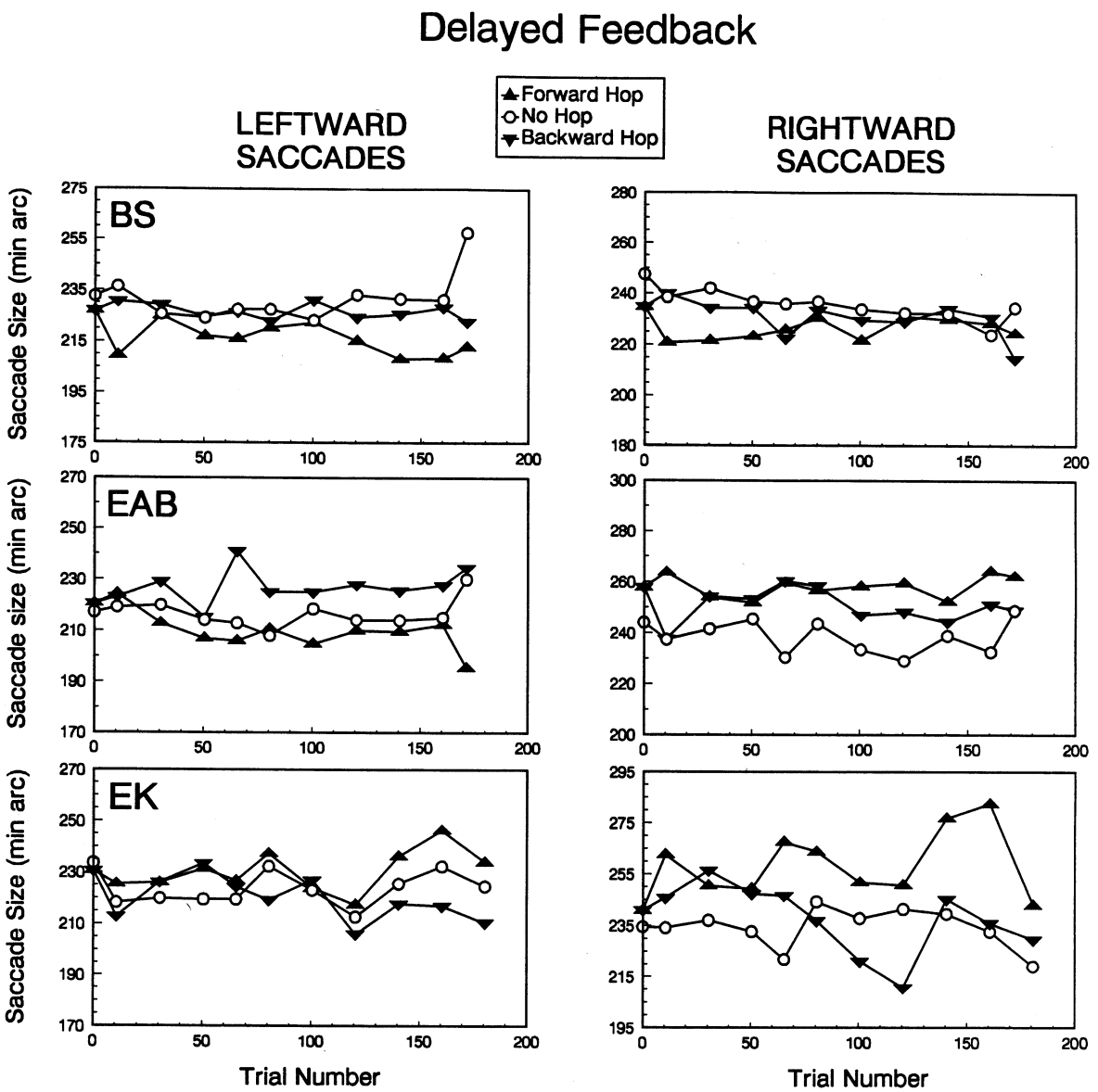

Fig. 8. Mean saccade size as a function of trial number in the experiment where appearance of the post-saccadic target was delayed 400 ms. Data are shown for three subjects, two saccadic directions and three hop conditions (forward, backward, and no-hop). Each symbol shows saccade size averaged over 20 consecutive trials. Data are shown for three subjects and two saccadic directions. Perceptual localization trials (not shown) were periodically interspersed after trial 90 (Bahcall & Kowler, 1999). The symbol at trial 0 shows saccade size averaged over the 20 no-hop trials which preceded each session.

uli, a green cross, hopped backward while the other stimulus, a red circle, remained stationary. Despite the different hops directions associated with the two shapes, saccades showed similar patterns of adaptation for the two stimuli. Deubel concluded that selective adaptation based on simple stimulus features is not possible. In Deubel's experiment only one of the shapes hopped while the other shape remained stationary. We produced a stronger dissociation between two different-shaped targets by having them hop in opposite directions so that accurate saccades to each would require adaptive changes.

The two shapes were a square and a diamond, each composed of 12 points evenly spaced around the perimeter of a 1° square (the diamond was created by rotating the square 45°). The shapes were randomly intermixed within an experimental session, with the square always hopping forward, and the diamond always hopping backward. The size of the hops (48′) was the same as that used in the prior experiments. The length of an experimental session was increased in order to have enough trials for each stimulus shape. EK was run in blocks of 390 trials which contained 40 baseline no hop trials, 300 adaptation trials (squares hopped

forward, diamonds hopped backward) and 50 post-adaptation no-hop trials. The target shape (square or diamond) was selected randomly on each trial with the restriction that on every ten trials there be five squares and five diamonds. BS ran in shorter sessions containing 40 baseline trials, 140 adaptation trials, and 40 post-adaptation trials.

The results are shown in Fig. 9 and summarized in Fig. 10. There was little overall difference between saccades made to the square and diamond. There was, however, a hint of selectivity in EK's second replication where saccades made to the square were slightly larger than those made to the diamond, consistent with the direction in which the shapes were hopping. The results

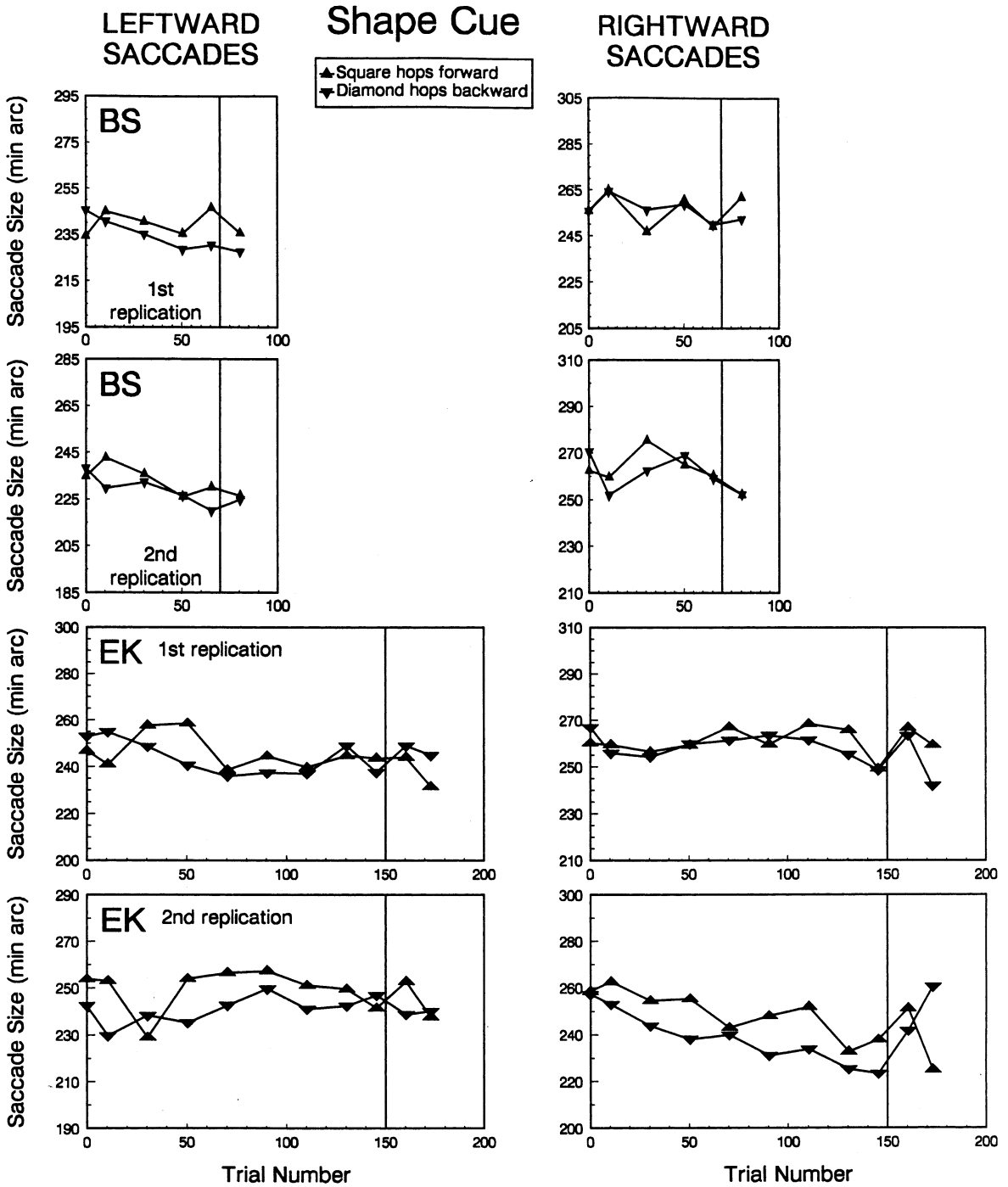

Fig. 9. Mean saccade size as a function of trial number for the shape cue experiment where a square stimulus hopped forward and a diamond hopped backwards. Data are shown for two replications for two subjects, two saccadic directions and three hop conditions (forward, backward, and no-hop). Each symbol shows saccade size averaged over 20 consecutive trials. The solid vertical line at trial 110 (BS) and trial 150 (EK) indicate when the adaptation trials ended and testing began with the post-adaptation no-hop trials.

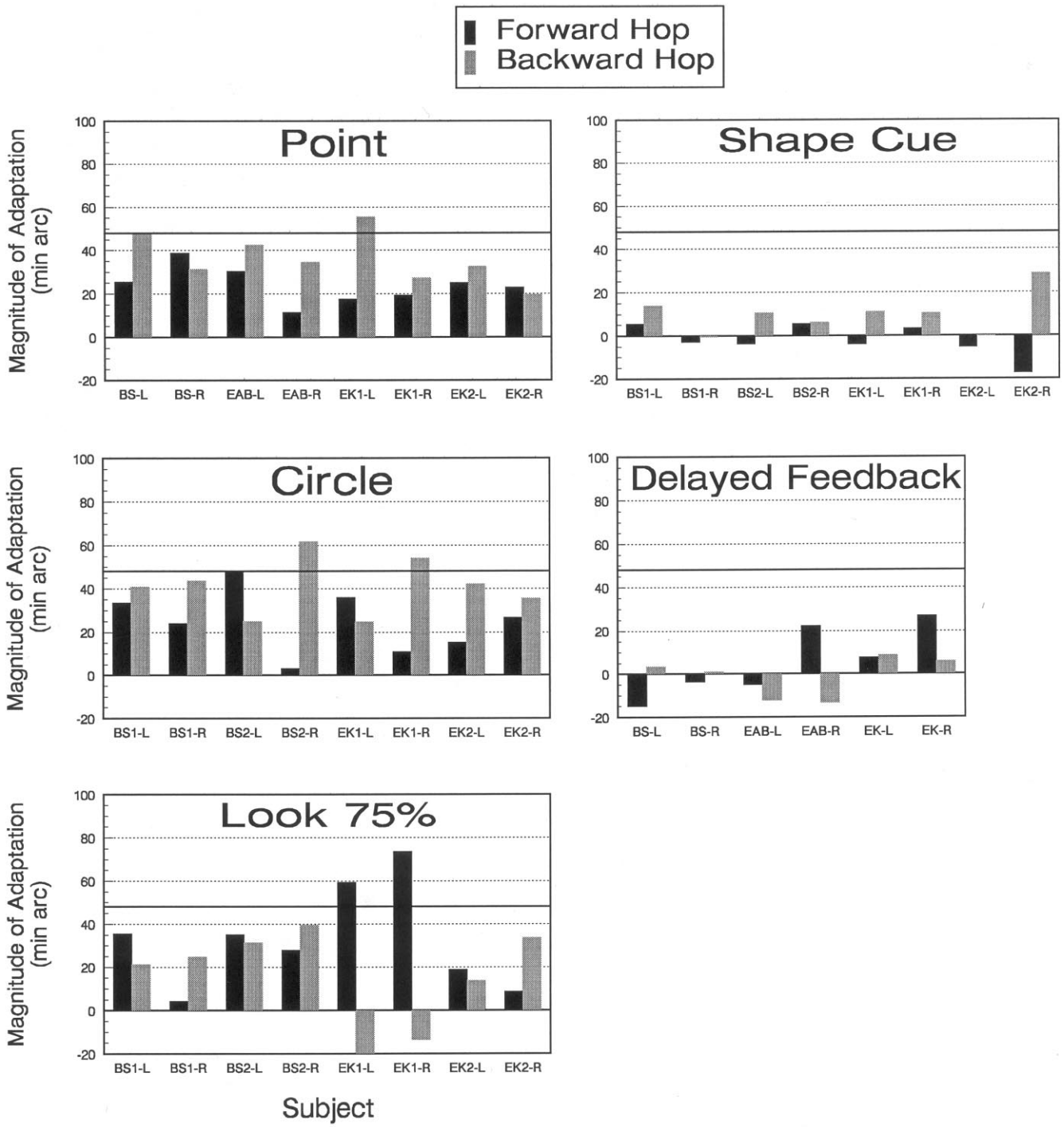

Fig. 10. Magnitude of saccadic adaptation for the forward and backward hop conditions of each of the experiments. Data are shown separately for each subject (BS, EAB and EK), replication (1, 2), and saccadic direction (left, right). The magnitude of adaptation was calculated as the difference in saccade size (averaged over the final 40 adaptation trials) between the forward and no-hop conditions, or the backward and no-hop conditions. The solid horizontal line at 48 min arc indicates the size of the intra-saccadic target hop. Positive values indicate adaptation in the direction of the hop.

suggest that, if the saccadic system is capable of selective adaptation based on high-level properties of the stimulus, it will require considerably more exposure than 140–390 consecutive trials/session tested here. This stands in contrast to the usual rapid rate of saccadic adaptation (Fig. 3) and rapid rate with which anticipatory smooth pursuit shows sensitivity to symbolic cues (Kowler, 1989).

4. Discussion

The phenomenon of saccadic adaptation shows that the saccadic system continually monitors its own performance, adjusting the relationship between the location of the visual target and the saccade, as needed, to ensure accurate movements. One error signal that could be used to assess saccadic accuracy is the retinal position error of the target (i.e. retinal distance between the target and the line of sight) when the saccade lands. However, as outlined in Section 1, it may be difficult to evaluate position error in natural scanning tasks. Position error is hard to define in natural environments, where targets are spatially-extended objects without visible landmarks denoting the expected landing position. Also, targets are surrounded by backgrounds, thus creating a host of possible visual position error signals that would have to be ignored by the system controlling adaptation. While neither of these difficulties is insurmountable, our results raise questions about the role of retinal position error in controlling the adaptation of saccades.

First, we found equivalent amounts of adaptation with a single point target and a large circle. This result is interesting because with the circle, position error would have to be defined with respect to a landmark derived from pooling information across the target. The difficulty in using such a derived landmark to control adaptation is that it must be computed both before the saccade (to provide the initial saccadic goal), and then re-computed after the saccade lands (to evaluate the error). Ideally, the location of the landmark should be the same in each case, despite the fact that visual information must be pooled over locations with different retinal eccentricities before and after the saccade.

We have evidence that the saccadic system does *not* re-compute the landmark after the saccade lands. Specifically, secondary, corrective saccades were virtually abolished with large target circles, but not with target points. Prior work has shown that corrective saccades become less frequent with increasing target size, becoming rare when targets are so large that the primary saccade lands within the boundary (Kowler & Blaser, 1995). The lack of corrections with large targets implies that the central landmark needed to evaluate retinal position error and trigger corrections is no longer available once the line of sight lands inside the boundary and target eccentricity is reduced (Burbeck & Yap, 1990; Levi & Klein, 1990; Kowler & Blaser, 1995). If the central landmark is not available to evaluate position error, and yet saccadic adaptation proceeds in the usual way, then either the adaptive system has a way to circumvent the limitations of the large target size and small target eccentricity when computing retinal position error, or it uses a different kind of error signal.

Further evidence against a prominent role for retinal position error came from the experiment in which subjects were instructed to look 75% of the way to the target. Under this condition, the retinal eccentricity of the target after the saccade took on values ranging from zero (with the backward hops), to about 60′ (with no-hop) or 110′ (with forward hops). Yet adaptation proceeded as it typically does, with little change in saccades during no-hop sessions, increases in saccadic amplitude in forward hop sessions and decreases in backward hop sessions. The variability of saccadic performance increased, but this might not be too surprising given the difficulties expected when trying to maintain a stable criterion for defining 75% of the way to the target. These results show that adaptation is related to the hop and not to the retinal eccentricity of the target after the saccade.

The reduction in adaptation we found when the appearance of the post-saccadic target was delayed also argues against the importance of retinal position error. Under these conditions, the spatial parameters of the retinal position error signal were not altered. If adaptation were triggered by post-saccadic position error — the distance between the line of sight and the target — then adaptation should have been unaffected by the delay. Instead, the interference with adaptation suggests that visual processes involved in a comparison of pre- and post-saccadic images, which would be expected to be sensitive to imposed delays, are more important that the detection of position error by itself.

We also found that adaptation was insensitive to cues about the direction of the upcoming intra-saccadic hop. When square-shaped targets hopped forward and diamond-shaped targets hopped backwards, saccades showed little evidence of adapting at all. Instead, the random mixture of hop directions prevented the development of systematic adaptive shifts and performance did not differ much for the different target shapes. Deubel (1995) reported something similar for a random mixture of red and green targets, one hopping backwards, and the other not at all. In that case, adaptation in a backward direction was observed for both types of targets. Greater sensitivity to high-level cues about hop direction could, of course, appear with either different cues or more exposure. Such an outcome, however, would suggest that, in contrast to other aspects of oculomotor control (Kowler, 1989), high-level cues are not the natural means of controlling adaptation, which seems to depend more on the past history of performance.

4.1. What is the error signal for saccadic adaptation?

We found that saccadic adaptation: (1) was the same for point targets and large targets; (2) was not dependent upon corrective saccades; (3) was immune to delib-

erate adjustments in retinal offset; (4) was insensitive to symbolic cues; (5) was disrupted by delaying the appearance of the post-saccadic target. These results cast doubt on the contribution of three different types of error signals to saccadic adaptation: retinal position error (offset of the visual target), signals from corrective saccades, and cognitive cues. None was related in a straightforward way to the conditions that enabled, or the conditions that abolished, adaptive changes in saccades.

A promising alternative is the visual comparison model. According to this idea, adaptation depends on a comparison of two images: the retinal image after the saccade lands, with the image that would be predicted based on the size and direction of the planned saccade. A large discrepancy could generate an error signal that initiates the adaptive changes in saccades, changes that would continue until the post-saccadic image matched the prediction within some criterion. Such a comparison model is consistent with our findings because it would work equally well with large and small targets, it would not have to keep track of which object or location was selected as the saccadic goal, and it would not need to be sensitive to corrective saccades, cognitive strategies or symbolic cues. A comparison process would also be expected to suffer if the time interval between the images to be compared was too long.

The comparison model is supported by other evidence. Bahcall and Kowler (1999) found that saccadic adaptation affects the perceived location of targets. Targets flashed before and after saccades, separated by amounts comparable to the size of the adaptive changes in saccades, seemed to be in the same location. These illusory mislocalizations (which were not found with unadapted saccades) showed that the perceptual system does not have access to a signal representing the saccadic movement that was actually made. Instead, it is more likely that the perceptual judgments of location depended on a signal representing the saccade that was initially planned, generated at a high-level, before the site of the adaptive modifications. This same high-level signal can also provide the basis for predicting the location of the post-saccadic retinal image. Adaptive changes to saccades would then be initiated whenever mismatches between the predicted and actual images exceed a specified threshold. A visual comparison scheme was also proposed by Deubel (1991) based on findings of adaptation in response to the intra-saccadic displacements of a large textured pattern.

There is physiological support for the idea that signals representing saccadic plans are used to predict the future, post-saccadic location of images. Receptive fields of cells in partial cortex change their location just before the saccade begins, shifting to the location of the stimulus that is expected to fall into the receptive field (Duhamel, Colby & Goldberg, 1992).

According to the visual comparison model, saccadic adaptation is not based on a static position error, but rather on motion: the comparison of two different images (the post-saccadic image and the pre-saccadic prediction) available sequentially in time. The interesting aspect of controlling saccadic adaptation by a retinal motion signal is that retinal motion is also responsible for adaptation of the vestibulo-ocular response (VOR). Adaptation of the VOR is initiated when oculomotor compensation for movements of the head is inadequate, resulting in too much image motion on the retina every time the head moves (Collewijn, Martins & Steinman, 1983; Melvill Jones, 1985).

Linking adaptation of the VOR and adaptation of saccades may be of some significance. Saccadic adaptation is usually viewed as a means of compensating for errors that occur due to disorders, wear-and-tear, or other changes in the saccadic system, or due simply to neural noise. Another source of saccadic error, one that is particularly important in natural tasks, is inappropriate coordination of the movements of eye and head. The initial command to look at a selected object while the head is free to move is most likely a command to shift gaze, leaving it to lower-level centers to determine the relative contribution of eye and head (Zingale & Kowler, 1987; André-Deshays, Berthoz & Revel, 1988; Freedman & Sparks, 1997). Gaze shifts are extremely accurate, showing that the separate contributions of head and eye can be assigned without much error (Collewijn, Steinman, Erkelens, Pizlo & Van der Steen, 1992). Recent studies suggest that eye-head coordination in natural tasks depends in part on continual adjustment of the VOR gain, which affects both inter-saccadic image motion, as well as the size and dynamics of the saccades themselves (Epelboim, 1998). Perhaps signals representing retinal image motion, obtained both across saccades and also during intersaccadic intervals, are used to adjust VOR gain, in concert with other parameters relevant to saccades, to produce both accurate gaze shifts and an appropriately stable retinal image at the same time. According to this view, the important function of saccadic adaptation in natural tasks is not to compensate for damage or random error, but to coordinate the programming of eye and head movements during shifts of gaze.

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